A NEW GENUS AND SPECIES OF PLIOCENE BOSELAPHINE (BOVIDAE, MAMMALIA) FROM SOUTH AFRICA

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(With 28 figures and 4 tables)

CONTENTS

INTRODUCTION

One of the more remarkable mammalian species from the Pliocene deposits at Langebaanweg in the Cape Province (Hendey 1970*a*, 1970*b*) is a hitherto unknown boselaphine. It is only recently that representatives of this tribe have become known in Africa at all, and this is their most southerly record.

Since reference to the Langebaanweg boselaphine was first made (Gentry *in* Hendey 1970*a*: 114), new material has been recovered and it is now possible to give a more comprehensive account of its characteristics and affinities. All the new material is from Bed 2, 'E' Quarry, and it is probable that the original 'E' Quarry specimens were also from this bed. It is thus an element of a fauna correlated with 4–5-million-year-old East African faunas (Hendey 1970*b*, 1972, 1973).

SYSTEMATICS

Family **Bovidae** Gray

Subfamily **Bovinae** Gill

Tribe **Boselaphini** Simpson

Diagnosis

Tendency for skulls to be lower and wider than in other antelopes; horn cores often with keels but never with transverse ridges, inserted above or just behind the orbits; cranium little angled on axis of the face; braincase not very shortened; frontals between the horn bases generally not far above the level

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of the dorsal orbital rims and sometimes with internal sinuses; strong temporal ridges behind the horn cores; small supraorbital pits; low infraorbital foramen; median indentation at the back of the palate behind the level of the lateral ones; posteriorly the ventral edge of the auditory bulla passes upwards to meet the paraoccipital process; entire occipital surface in one plane facing backwards; brachyodont cheek teeth; rugose enamel; lower molars generally without anterior transverse folds (goat folds); long premolar rows; I_1s more enlarged than the other incisors or the incisiform canine; depth of mandible beneath the molars does not greatly exceed that beneath the premolars. (Modified from Gentry 1970: 245.)

Remarks

Boselaphini are bush or open woodland antelopes. The only two living forms are inhabitants of the Indian subcontinent: the nilgai *Boselaphus tragocamelus* (Pallas, 1766) and the much smaller four-horned antelope *Tetracerus quadricornis* (Blainville, 1816), but there are many fossil species in Eurasia particularly in the Siwaliks Hills of India and Pakistan, and it is becoming evident that the tribe has also occurred in Africa in the past. The Langebaanweg boselaphine will be defined as a new genus and species.

Mesembriportax n. gen.

Type species

Mesembriportax acrae n. sp.

Generic Diagnosis

The type species is the only member of the genus, and a diagnosis is given under the species.

Mesembriportax acrae n. sp.

Holotype

L 13101—a skull with mandibles, and associated vertebral column, rib fragments and right scapula (Figs 1, 2, 3, 5, 7, 8, 9, 10, 14, 15).

Referred Material

L 20508—Right mandibular fragment with P_2 to M_3, left mandibular fragment with M_1 to M_3, and associated vertebrae, rib fragments, left metacarpal fragment, left femur fragment, left lateral malleolus, left metatarsal, one 1st phalanx and three 3rd phalanges (Figs 10, 11, 21, 22, 23).

L 20509—Skull fragments including the right horn core (Fig. 4).

L 13106—Skull fragments including parts of the right horn core (Fig. 5).

L 20506—Skull fragments including left P^2 and P^4 to M^3, right M^1 and M^2, left mandibular fragment with M_1 to M_3 and incompletely erupted P_4, associated with some fragmentary vertebrae.

L 14251—Left and right horn cores (Fig. 4).

L 3003, L 4657, L 5692, L 5923, L 6587, L 12757, L 12758, L 12812, L 12813, L 13141, L 13193, L 20234—Horn core fragments.

Upper teeth as follows:

L 6450—Left and right P^2 and parts of P^3; L 10933—left M^3; L 10941/6—right M^1 to M^3 and left P^2 and M^1; L 12861—right M^1 and M^2; L 12862—left and right M^3; L 13111—right P^2 and P^3; L 13140—right P^3 and M^2 and other fragments; L 14314—left P^2; L 14465—left M^2 and M^*; L 20536—left M^3 and other fragments.

Mandibular fragments as follows:

L 6601—With left P_4 to M_3; L 11821—with left M_1 and M_2; L 12860—with right P_4 to M_3; L 13136—with left P_3 to M_1 and part of M_2; L 13139—with right P_2 to M_3; L 14200—with right M_1 to M_3 and left P_3; L 14257—with right P_3 to M_3 and left P_2 and M_1; L 20405—with right M_1 and M_2 and parts of P_4 and M_3; L 20534—with right M_1, M_2 and part of M_3; L 20538/9—with incomplete left P_4 to M_3 and right P_2 to M_3.

Lower teeth as follows:

L 10924—Left M_1 and M_2; L 10936—left P_2; L 11979—right P_4; L 12698—right M_2.

The following are juvenile remains:

L 11000/2—Left mandibular fragment with dP_2 to dP_4, M_1 and M_2, and unerupted P_3 and P_4; right dP_4, M_1 to M_3, and unerupted P_2 to P_4.

L 14202/3—Left mandibular fragment with dP_4 and unerupted M_1 and left maxillary fragment with crushed dentition.

L 14237—Left mandibular fragment with dP_4 and unerupted M_1.

L 20688—Left and right mandibular fragments with dP_2 to dP_4 and incompletely erupted M_1; left maxillary fragment with dP^2 to dP^4 and incompletely erupted M^1. This material is possibly associated with a number of postcranial bones found nearby (Figs 12, 13).

Tentatively referred material

L 13197—Left scapula (Figs 16, 17).

L 13071—Right humerus, radius, ulna, scaphoid, lunate and metacarpal (Figs 18–22).

L 7625 —Right metatarsal (Figs 21, 22).

L 20334—Right metatarsal.

L 14081—3rd phalanx.

The holotype and all other material is housed in the South African Museum, Cape Town.

Locality

Bed 2 of 'E' Quarry, Langebaanweg, Cape Province. In addition, a single horn core fragment (L 1588A) has been recorded from Baard's Quarry, Langebaanweg.

Age

Pliocene.

Diagnosis

A moderate to large-sized boselaphine; horn cores rather short, inserted fairly uprightly and widely apart, very divergent basally and slightly less so distally, strongly compressed medio-laterally and with a postero-lateral keel and a strong slightly helical anterior keel in their lower part, the anterior keel being stepped at its top and the succeeding distal part of the horn core being of small circular cross-section. Frontals extensively hollowed internally, and their top surface raised much above the level of the top of the orbits; braincase slightly angled on the face axis; top of braincase not curved downwards posteriorly above the occipital surface; strong temporal ridges on braincase roof approaching posteriorly and with a rugose surface between them; braincase widening posteriorly; orbits without a projecting dorsal rim; small supraorbital pits; nasals long and narrow with large central flanges anteriorly but no lateral flanges; large preorbital fossa; infraorbital foramen low and situated above the posterior margin of P^2; premaxillae narrow anteriorly but with strong ascending rami of approximately even width throughout and with a wide contact on the nasals; palate very wide; median indentation at the back of the palate well behind the level of the lateral indentations; large mastoid exposure of periotic; anterior tuberosities of basioccipital fairly wide apart and not very large.

Brachyodont or only moderately hypsodont cheek teeth, with not very rugose enamel; small basal pillars on upper and lower molars; medial lobes of upper molars not joined to one another or to the lateral side of the tooth until late in life; mesostyles quite strong on upper molars; central cavities of upper molars not very complicated in outline; medial walls of lower molars rather flat; lower molars sometimes with small goat folds (a transverse flange at the front of the tooth); long premolar rows with large anterior premolars; paraconid and metaconid not fused or only just fused on P_4; projecting hypoconid on P_4; I_1s not greatly enlarged.

Name

The generic name is made from μεσημβρῖνός (mesembrinos) southern, and πόρταξ (portax) a calf, the latter word being a frequent constituent of boselaphine names. The specific name is from ἀκρα (acra) a cape, and is given as a Latinized genitive singular.

The Skull

The holotype skull is largely complete, but owing to some distortion in the facial region it is in three separate parts—the cranium with horn cores, the

Fig. 1. L 13101, holotype of *Mesembriportax acrae*. Lateral view of cranium.
Scale in all photographic figures is in centimetres.

palate, and the remainder of the face region. Part of the occipital, the auditory bullae and other more delicate parts of the basicranium are lost, as is much of the right horn core and parts of the left. Some pieces, especially of the frontals, could not be restored to the skull. The dentition is complete except for some small pieces missing from the upper and lower cheek teeth.

The horn cores are large, without transverse ridges, not curved backwards, and inserted above the back of the orbits. They have an ovate cross-section in their basal part. The anterior keel is very pronounced, and terminates well below the tip of the core. The torsion in the horn cores is anticlockwise from the base up on the right side, and it results in the termination of the anterior keel being situated at what has become the lateral edge of the horn core. Proximally the keel becomes very sharp-edged, a feature which is best seen in the specimen L 13106. The postero-lateral edge is also keeled, while the postero-

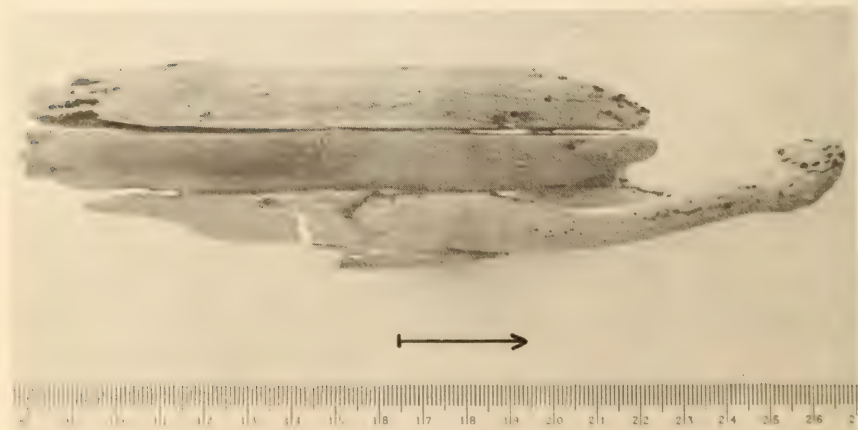Fig. 2. L 13101, holotype. Anterior view of cranium.

Fig. 3. L 13101, holotype. Dorsal view of nasals with right premaxilla and part of right maxilla; the arrow points anteriorly.

medial edge is rounded. There is some individual variation in shape of the proximal parts of the horn cores; in the holotype and others the medial and lateral surfaces of the lower part of the horn cores are slightly convex and widely angled on the posterior surface, which is also convex, but in L 13106 the postero-lateral keel is more prominent, the posterior surface less rounded, and the lateral surface flatter. In L 4657 and L 20509 there are well-developed grooves running along most of the posterior surfaces of the horn cores. Distally from the termination of the anterior keel the horn core becomes much smaller with a circular cross-section and in this region the horn cores are less widely divergent. The relative length of this distal portion appears to vary considerably as can be seen from Figs 1, 2 and 4.

There are ridges of bone extending antero-medially across the frontals from the anterior keels of the horn cores. Since this region of the skull is incomplete in all specimens it is not known how closely the ridges approach one another. The supraorbital pits are preserved only on the holotype, where they are very small. There is almost no sign of a postcornual fossa postero-laterally to the horn pedicel. The internal hollowing of the frontals extends quite high into the horn pedicel. Extending posteriorly along the midline of the skull from the highest point of the frontals between the horn cores is a ridge of bone which terminates at or near the parieto-frontals suture.

Bohlin (1935) argued that the extinct Eurasian boselaphine *Miotragocerus* originally had horn cores of an elongated oval cross-section, and that later species of the genus evolved periodic growth at the anterior base of the horn core to produce a series of steps along the course of a sharp anterior keel. The horn cores acquired greater and greater antero-posterior diameters during the life-span of an individual. These phenomena may not have occurred in all *Miotragocerus*, and *M. browni* and the Samos skulls named *M. curvicornis* (Andree 1926) and *M. recticornis* (Andree 1926) are obviously difficult specimens in which to visualize them. Thenius (1948) commented that this method of horn core growth did not necessitate periodic sheddings of the horn sheath provided that sheath growth was as in other bovids. He thought that a bifurcated sheath like that of the North American pronghorn, *Antilocapra americana*, may have occurred in *Miotragocerus*. There is no indication of steps along the course of the anterior keel in *Mesembriportax acrae*, except just possibly in L 13106, but one can scarcely imagine it not having a bifurcated sheath at the point where the anterior keel disappeared. This, coupled with the very wide divergence of the horn cores, suggests that males would have fought by grappling, a method of combat different from the pushing and neck fighting of living *Boselaphus* (Walther 1958: 358). The four horns of the living *Tetracerus quadricornis* provide a precedent for anomalous horn features among the Boselaphini.

The thick frontals with their extensive internal sinuses are one of the most notable characters of *M. acrae*. Such sinuses and struts occur in the males of advanced species of Caprini, and help to protect the brain from the ramming and clashing of the very large horns (Schaffer & Reed 1972: 47). In *M. acrae*
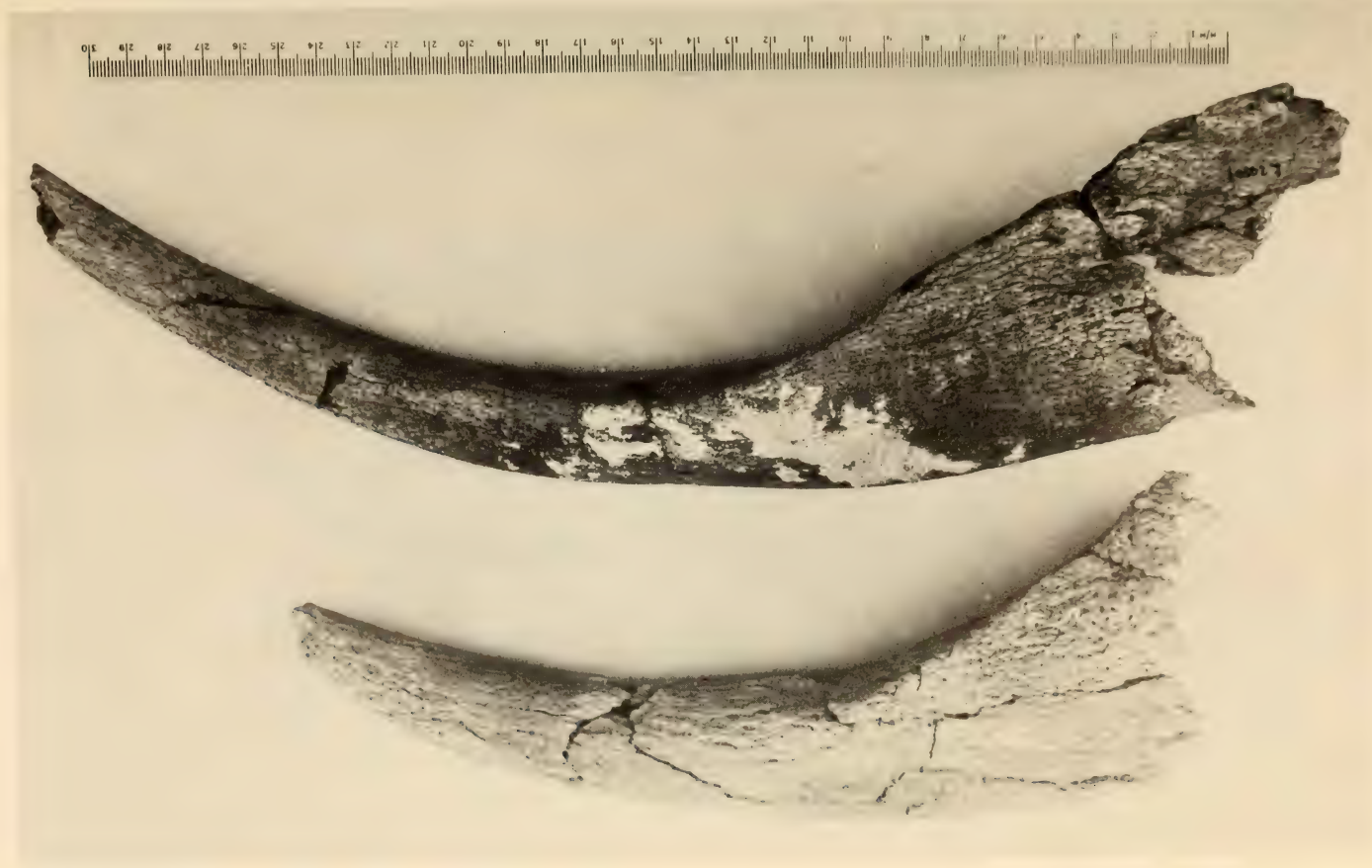
Fig. 4. Antero-lateral views of right horn cores L 14251 (on the left) and L 20509 (on the right).

anterior

↑
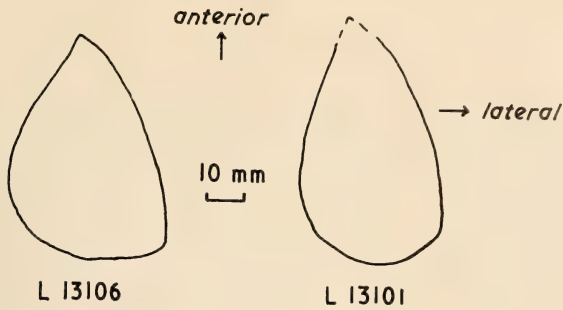
→ lateral

10 mm

L 13106   L 13101

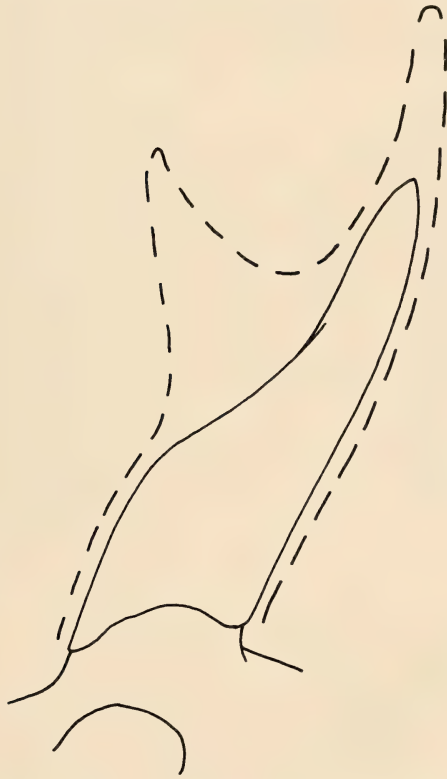Fig. 5. Cross-sections of two horn cores near their bases.

Fig. 6. Diagram of a bifurcated horn sheath (dashed lines) fitted over a horn core of *Mesembriportax acrae*.

they may have protected the brain against the hypothetical horn prongs but were more probably connected with the support of the very divergent and over-hanging horns. Such divergent horns may have needed additional bracing to prevent them being too easily snapped during the grappling and pushing between males. The dorso-ventral height of the frontals, irrespective of whether or not

they possessed sinuses, may also have been a means of raising the horns above the level of the orbits, thus giving some protection to the eyes and avoiding interference with the field of vision.

It is not known whether or not the females of *M. acrae* had horns; if the species were like other boselaphines in which the state of this character is known, they did not.

The temporal ridges of *M. acrae* arise from the postero-medial edge of the horn core pedicels, and converge towards the nuchal crest, although they remain fairly wide apart at their posterior termination. The roof of the brain-case is flattened in the nuchal region. Arising from the temporal ridges about midway along their length and extending postero-medially are two swellings in the bone which converge about half-way along the surface of the braincase. Anteriorly from these swellings about as far as the parieto-frontals suture, the roof of the braincase is slightly concave and there is a marked rugosity of the bone in this region.

The braincase is broad and rather low, and its roof meets the occipital at an angle of approximately 90°. The nuchal crests are not very prominent; laterally they are directed slightly anteriorly and terminate in large, somewhat bulbous paraoccipital processes. The skull is less wide across the occipital surface than across the orbits. The posterior tuberosities of the basioccipital are fairly prominent, but the anterior tuberosities are small, and there is a slight narrowing of the basioccipital anteriorly. A central longitudinal groove is seen only between the posterior tuberosities, and between the anterior tuberosites there is even a central ridge. The middle of the basioccipital is not transversely constricted.

The preorbital fossae are extremely large, and the width of the face on either side of the narrow nasals is about the same as in the premaxillary region. There is a marked flaring outwards of the face from beneath the preorbital fossa to the alveolar margin of the tooth row. Although this is to some extent a character of all boselaphines, it appears to be exceptionally pronounced in *M. acrae*. The palate is very broad, particularly at the molar rows, and the P⁴s are in fact stepped in from the level of the M¹s.

The upper molars are large and typically boselaphine in morphology, and all have small basal pillars which are variably developed. In some cases there are two individual pillars on each tooth and in others only one. In the holotype the M³s have projections from the most postero-lateral parts of the cingulum. This feature has not been noted in any other boselaphine specimen, nor is it present in other Langebaanweg M³s. The upper molars are very broad, the M¹ being appreciably broader at its base than it is long, the M² being slightly broader than long, and the M³ having its breadth approximately equal to its length. The joining of the two medial lobes of each upper molar to one another and to the lateral side of the tooth is possibly more advanced than in earlier boselaphines; in the holotype the junction is actually made but is very narrow in each case. The lower molars have small basal pillars decreasing in size from
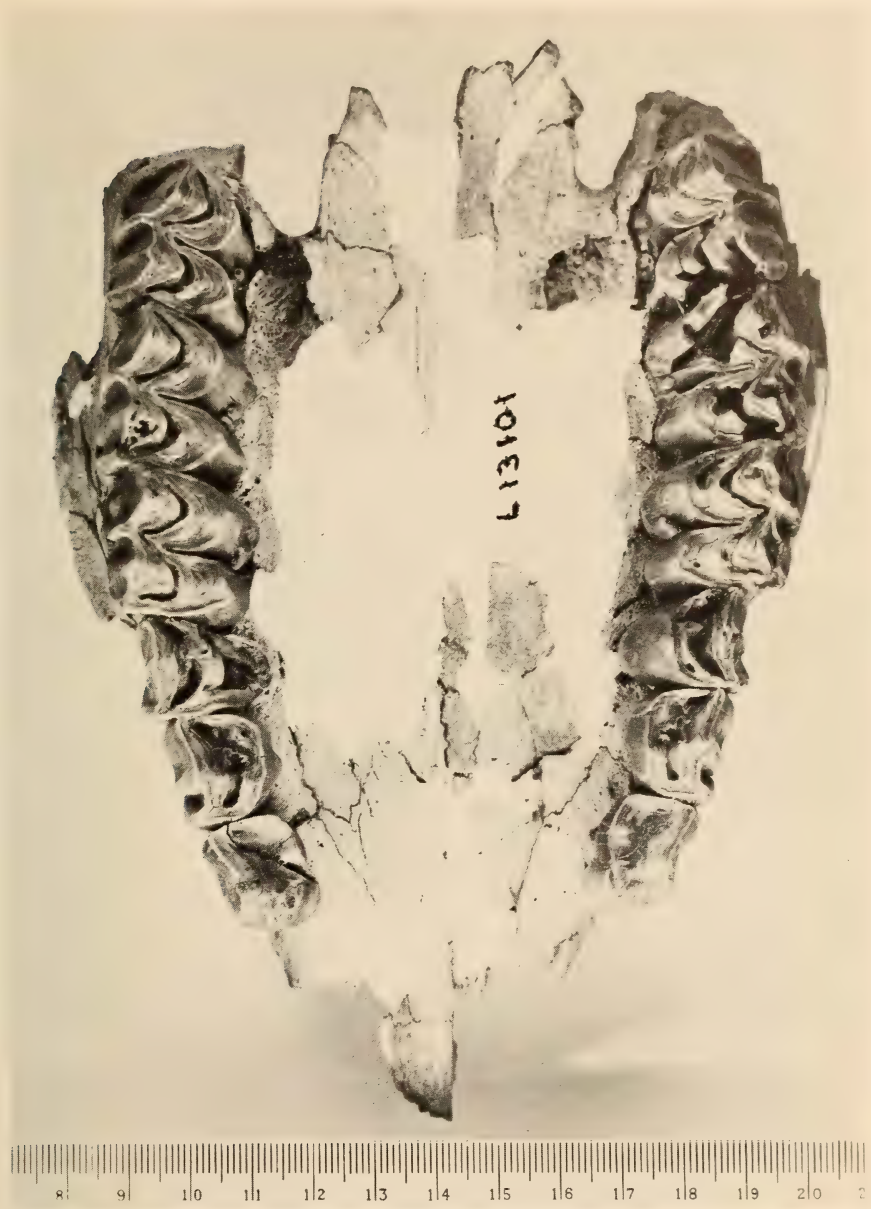
Fig. 7. L 13101, holotype. Palate.

M_1 to M_3. In the latter tooth there is an additional basal pillar between the middle and the posterior lobes, rather smaller than the main one. The transverse anterior goat folds are poor on the holotype, but stronger in some other lower dentitions which are in an earlier stage of wear, e.g. L 11000. There is a large

Fig. 8. L 13101, holotype. Lateral view of left mandible.

Fig. 9. L 13101, holotype. Occlusal view of left incisors.

metaconid on P_4 and it approaches closely to the paraconid in the holotype but without fusion. In L 20508 the fusion has taken place but is not strong. The central incisors, I_1s, are the largest of the symphyseal teeth, but are probably smaller in relation to I_2, I_3 and C than in the earlier *Protragocerus labidotus* from Fort Ternan, Kenya.

The mandibular diastema is about as long as the lower molar row. The mandibular corpus is relatively shallow and deepens only slightly beneath the tooth row. The ascending ramus rises steeply, almost at right angles immediately behind the M_3, and its anterior edge and posterior edge below the condyle are nearly parallel. The two anterior deciduous premolars of both the upper and

Fig. 10. Occlusal view of lower dentitions. Above: L 13101, holotype. Below: L 20508.

Fig. 11. Lateral view of left mandible L 20508.

lower dentitions are rather long. The dP^3 is a little-advanced tooth in which the shape of the front lobe is quite dissimilar to the back lobe. The dP$_4$ has two basal pillars.

The teeth of *M. acrae* agree well with other boselaphines and are not very different from those of Tragelaphini (eland, kudu, bushbuck tribe), so it is reasonable to suppose that this species fed at least partly by browsing. There is a great contrast in almost every character with the teeth of grazing antelopes such as the Alcelaphini (wildebeest and hartebeest tribe).

Measurements in millimetres on the holotype skull are:

Total length of horn core along anterior keel . . . . . . estimated 370
Total length of horn core along medial curve . . . . . . estimated 305
Anterior-posterior diameter at base of horn core at right angles to its longitudinal axis 69,1
Latero-medial diameter at base of horn core at right angles to its longitudinal axis 43,1
Minimum width across lateral sides of horn pedicels . . . . estimated 145
Length of nasals . . . . estimated 142
Skull width across mastoids behind external auditory meatus 122
Distance between outer edges of occipital condyles 65,0
Width across anterior tuberosities of basioccipital 26,8
Width across posterior tuberosities of basioccipital 33,0
Minimum width of palate between medial borders of M^{3}s 62,5
Occlusal length M^1–M^3 74,6
Occlusal length M^2 27,7
Occlusal length P^2–P^4 55,3
Occlusal length P^2 21,9
Occlusal length P^4 16,0
Occlusal length M$_1$–M$_3$ 80,7
Occlusal length M$_2$ 24,9
Occlusal length M$_3$ 34,6
Occlusal length P$_2$–P$_4$ 54,8
Occlusal length P$_2$ 16,1
Occlusal length P$_4$ 20,4
Overall length of mandible from anterior alveolar margin of I$_1$ to posterior limit of
    angle . . . . estimated 313
Diastema length . . . . estimated 77,0
Depth of mandibular ramus below P$_2$ 34,0
Depth of mandibular ramus below centre of M$_1$ 40,7
Depth of mandibular ramus below centre of M$_3$ 45,3
Height of ascending ramus between inferior margin and condyle 115

The following additional horn core readings were taken:

	Length along anterior keel	Length along medial curve	Antero-posterior basal diameter	Latero-medial basal diameter
L 4657	—	—	c.65,0	c.41,0
L 13106	—	—	61,7	40,0
L 14251	c.270	c.230	71,5	51,7
L 20509	c.380	c.310	c.74,0	42,4

The distance between the outer edges of the occipital condyles on L 20509 was c.74,0.

Measurements on adult upper teeth were:

L 12861	length M^2	c.26,5		
L 14465	length M^2	27,1		
L 20506	length M^2	24,9	length P^4	13,8

Measurements on lower dentitions are shown in Table 1.

Table 1

	L 6601	L 10924	L 11821	L 11979	L 12860	L 13139	L 14200	L 14257	L 20405	L 20506	L 20508	L 20534	L 20539
Occlusal length M_1–M_3	73,5	—	—	—	*c.*75,5	*c.*72,0	—	*c.*73,0	—	—	74,7	—	78,4
,, ,, M_2	23,7	24,7	25,4	—	24,1	*c.*24,0	25,8	24,7	24,3	25,1	23,7	24,6	25,2
,, ,, M_3	30,1	—	—	—	32,3	*c.*31,0	33,1	31,0	—	*c.*34,0	31,1	—	35,2
,, ,, P_2–P_4	—	—	—	—	—	53,9	—	—	—	—	53,1	—	*c.*56,0
,, ,, P_2	—	—	—	—	—	15,8	—	—	—	—	15,2	—	15,9
,, ,, P_4	20,3	—	—	19,1	*c.*19,7	19,8	—	18,5	—	—	20,0	—	*c.*21,3
Ramus depth below P_2	—	—	—	—	—	—	—	—	—	—	32,5	—	36,5
,, ,, ,, M_1	—	—	—	—	38,0	—	—	—	32,3	—	35,2	36,6	*c.*45,0
,, ,, ,, M_3	—	—	—	—	*c.*40,5	—	—	—	36,9	—	38,6	38,8	*c.*48,5
Height of ascending ramus between inferior margin and condyle	—	—	—	—	—	—	—	—	—	—	97,0	—	—

Occlusal lengths of deciduous teeth were:

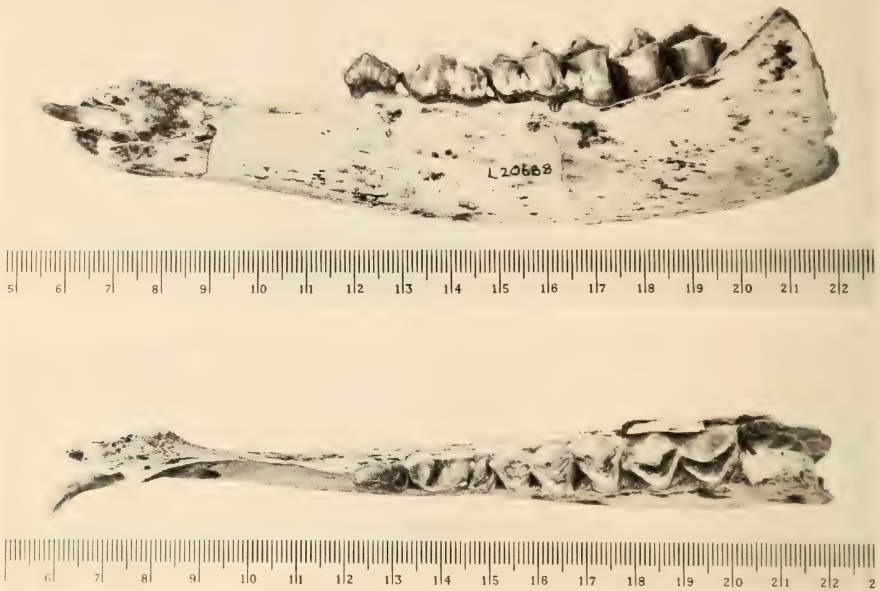|	dP2	dP3	dP4	dP2–dP4
L 20688 upper	20,9	21,9	21,4	60,1
L 20688 lower	11,8	18,0	28,1	56,4
L 11000 lower	12,7	17,7	c.25,0	—
L 14202 lower	—	—	27,1	—
L 14237 lower	—	—	25,0	—

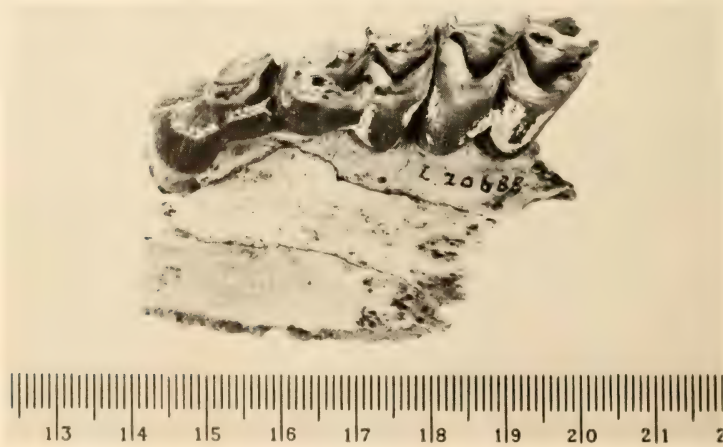Fig. 12. L 20688, immature left dentitions. Lateral and occlusal views of mandible with dP_2–M_1.

Fig. 13. L 20688, immature left dentitions. Occlusal view of maxilla with dP^2–dP^4.

Fig. 14. L 13101, holotype. Dorsal view of atlas vertebra.

Fig. 15. L 13101, holotype. Lateral view of axis vertebra.

Postcranial skeleton

A large number of bovid postcranial bones has been recovered from Bed 2 in 'E' Quarry, but only a few were associated with *Mesembriportax acrae* cranial remains and thereby positively identified with this species. Apart from

Fig. 16. L 13197, left scapula in lateral view.
See text for explanation of letters in Figs 16–22.

those bones associated with the holotype skull and the cranial elements L 20506 and L 20508, a number of other specimens (L 13197, L 7625, L 20334, L 14081) can be tentatively referred to *M. acrae* because they are very similar to positively identified material. The same applies in the case of a metacarpal which was one element of an incomplete right limb (L 13071). It is possible that L 13071 and
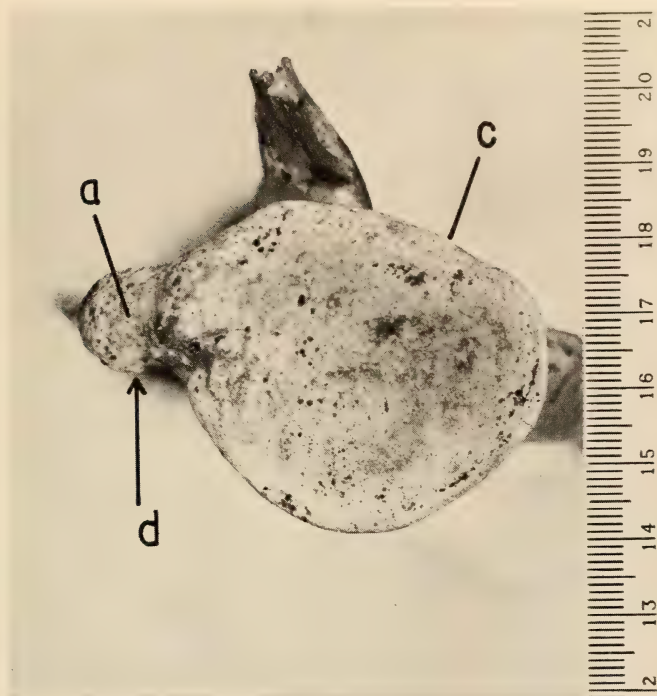
Fig. 17. L 13197, left scapula. Glenoid facet in ventral view.

L 13197 belong to the same individual since they were found close together.

Comparison of the postcranial material with extant antelopes is hampered by the poor samples of the latter—generally not more than two or three individuals of any one species. On their own, none of the fossil postcranial bones can be identified at generic or specific level. In many characters they resemble living tragelaphines, particularly the similarly-sized greater kudu (*Tragelaphus strepsiceros* (Pallas, 1766)), and are distinguishable from comparable elements of alcelaphines. The latter have a morphology suitable for more cursorial forms in an open plains habitat and Gentry (1970: 277–282) has listed and briefly discussed limb bone characters to be expected in such cursorial antelopes. A few cursorial features do appear in *M. acrae*, and it could have been an animal of open woodland. A greater number of cursorial characters appear in the nilgai, also an animal of open woodland, either because it has a slightly different ecological niche, or because it has evolved better adaptations in the last few million years.

The vertebral column associated with the holotype skull is complete as far as the sacrum, comprising seven cervicals, fourteen thoracics and five lumbars. In general the preservation of the individual vertebrae is good although many have lost the processes and other more delicate parts. The atlas and axis are the least well preserved. The atlas has a well-indented dorsal edge anteriorly
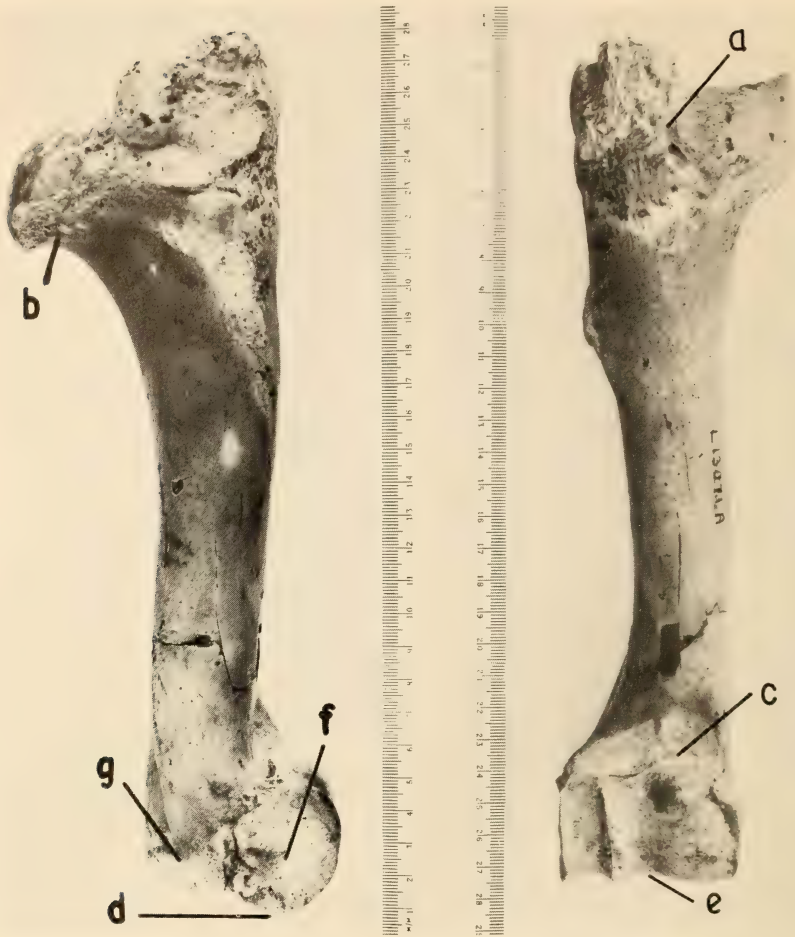
Fig. 18. L 13071. From the left: lateral view of right humerus, anterior view of same.

for articulation with the skull. It is unlike alcelaphines in having no projecting point in the middle of the ventral edge anteriorly, and in having convex rather than concave lateral edges. In these characters it resembles tragelaphines. On the axis the front edge of the neural spine does not pass very far forwards, and on the third and fourth cervicals there are widely separated openings of the vertebrarterial canals. The other vertebrae are not distinctive in any way and those of the referred specimens (L 20506, L 20508) are essentially similar to those of the holotype.

The scapulae of the holotype and the referred specimen, L 13197, have quite small tubera scapulae (a, Fig. 17) in ventral view, with their bases situated above the level of the rims of the glenoid facets in lateral view (b, Fig. 16). The glenoid facets have no indentations in their lateral edges (c, Fig. 17). All these characters
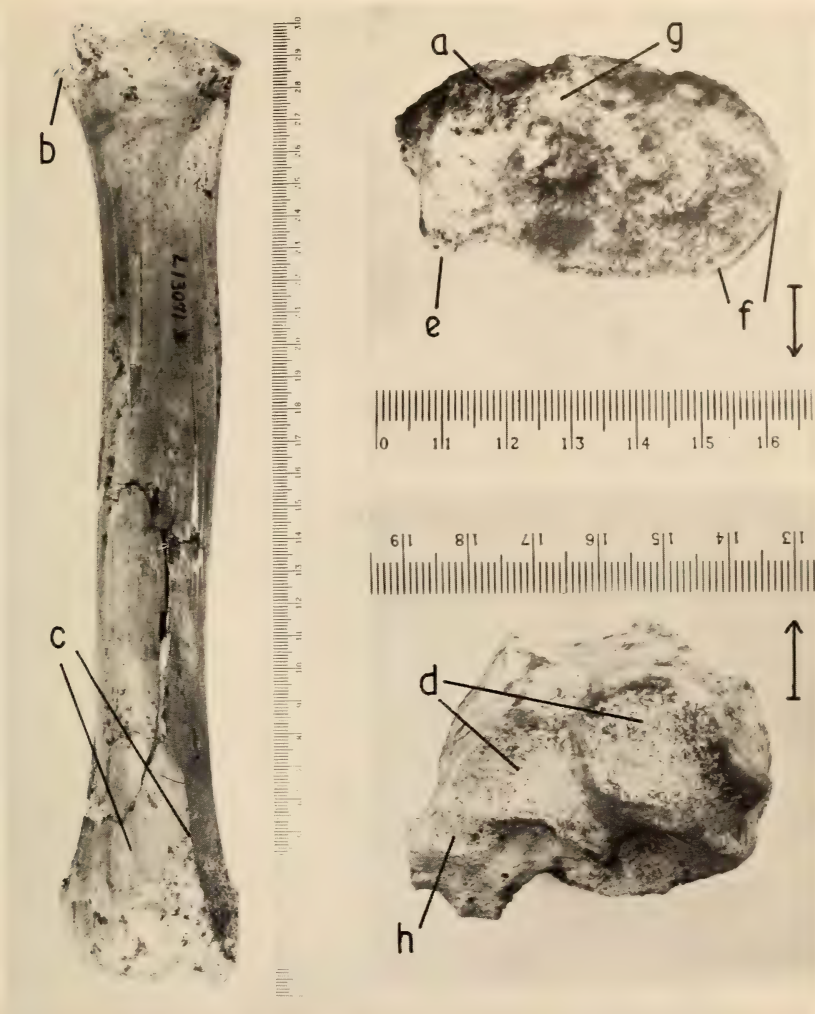
Fig. 19. L 13071, right radius. Left: anterior view. Right above: proximal articular surface.
Right below: distal articular surface.
Arrows point anteriorly.

differ from the condition of alcelaphine antelopes, but the lateral rather than the central position of the tubera scapulae in ventral view (d, Fig. 17) is not unlike alcelaphines. The nilgai has a larger tuber scapulae but is otherwise similar to *M. acrae*.

The humerus L 13071 has the front of its bicipital groove well anterior relative to the level of the front of the lateral tuberosity (a, Fig. 18), scarcely any hollowing for the brachialis insertion under the proximal articular head (b, Fig. 18), no indentation in the dorsal edge of the distal medial condyle

(c, Fig. 18), and no V-shaped ventral projection distally on its lateral side (d, Fig. 18). It is unlike alcelaphines in all these characters. The medial groove of the distal condyle is not very deeply incised (e, Fig. 18) and the distal hollow for the lateral humero-radial ligament is shallow (f, Fig. 18); these characters are also different from alcelaphines and were considered by Gentry (1970: 281) to be expected in non-cursorial bovids. However, the wide bicipital groove, upright distal condyle, and the high distal medial condyle of the fossil are characters of cursorial bovids. The back of the lateral side of the bone does not descend low behind the hollow for the humero-radial ligament (g, Fig. 18). The nilgai agrees with the Langebaanweg fossil only in four characters: the lack of an indented dorsal edge of the medial condyle, the shallow hollow for the humero-radial ligament, the wide bicipital groove and the upright distal condyle.

The radius has the back edge of the proximal lateral facet only a little forward of the level of the back of the medial facet (a, Fig. 19), the proximal lateral tubercle of small to moderate size and set rather low (b, Fig. 19), the distal end of the shaft swollen in lateral view, and wide flanges distally on the anterior surface (c, Fig. 19); all of these characters are unlike alcelaphines and most of them are unlike cursorial bovids generally. However the distal articular facets appear quite deeply incised (d, Fig. 19) to receive the proximal row of carpals, thereby tending to resemble cursorial antelopes. Other characters are a pointed front edge on the proximal lateral facet (e, Fig. 19), no angled medial or antero-medial corners on the proximal medial facet (f, Fig. 19), the postero-medial part of the medial facet projects quite strongly (g, Fig. 19), and the facet for the cuneiform is wide (h, Fig. 19). The nilgai agrees with the Langebaanweg fossil in the swollen distal end of the shaft and the wide flanges on the anterior surface, the deep distal articular facets, the wide cuneiform facet, and the characters of the outline of the proximal medial facet.

The scaphoid is deep, with an upper edge better indented than in the greater kudu but less well than in alcelaphines (a, Fig. 20), and it has no posterior prominence on its medial side (b, Fig. 20). All three characters are unlike alcelaphines, but the first and perhaps the second agree with the nilgai.

The lunate is without a strongly upstanding projection towards the back of its upper surface (c, Fig. 20), and has only shallow hollowings on its lateral (d, Fig. 20) and medial surfaces. Both characters are distinct from alcelaphines and the nilgai.

The metacarpals of L 13071 and that of L 20508, which lacks the lower half of the shaft and distal end, have relatively large unciform facets in comparison with the magnum-trapezoid facets (a, Fig. 22), the total proximal articular surface does not fill the entire available area at the top of the bone, and at the top of the distal condyles there are deep tiny hollows on the posterior surface. These characters are again unlike alcelaphines, and the first and last agree with the nilgai.

The femur of *M. acrae* is known only from a small part of the distal end (L 20508), which is too fragmentary to allow any description of its characters.
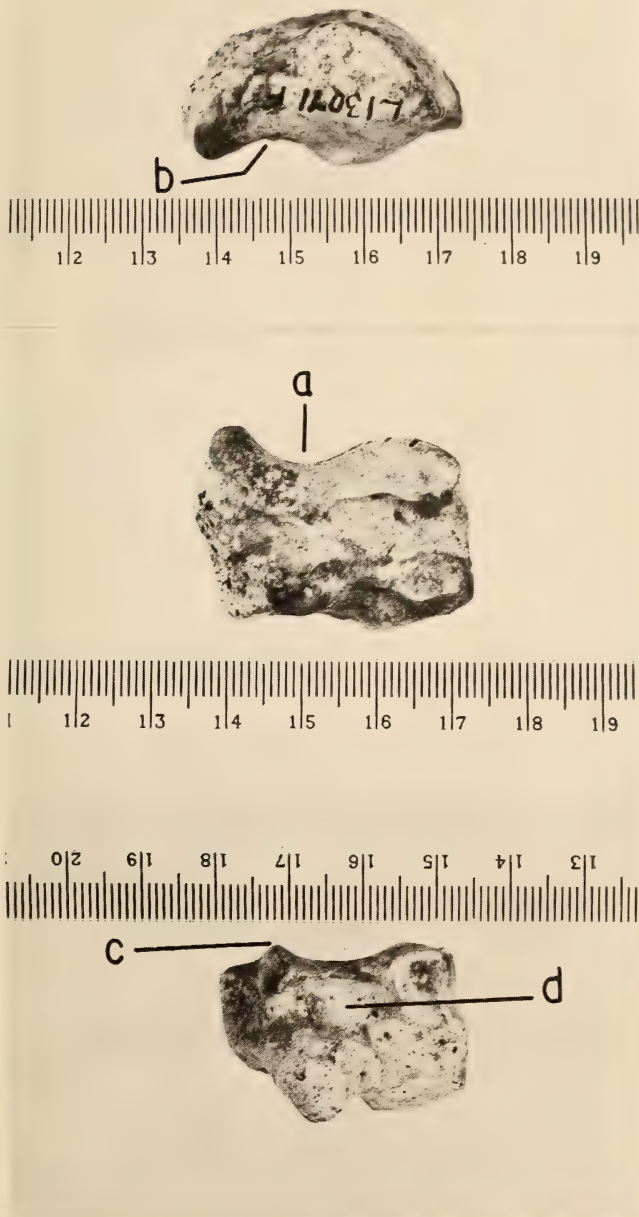
Fig. 20. L 13071. From above: dorsal view of right scaphoid, lateral view of right scaphoid, lateral view of right lunate. Anterior sides lie to the right.

Fig. 21. Anterior views of metapodials. From the left: L 13071 right metacarpal, L 7625 right metatarsal, L 20508 left metatarsal.

The innominate and tibia are not represented by any specimens which can be positively identified with this species and, with the exception of a single lateral malleolus (L 20508), no tarsal bones are recorded either. The lateral malleolus is similar to that of the greater kudu in overall size but is narrower and relatively more elongated antero-posteriorly. It is similar to the lateral malleolus of alcelaphines but unlike the nilgai in that the posterior end of the tibial facet curves ventrally and terminates on the posterior surface of the bone. A secondary, postero-ventrally situated medial facet of articulation with the astragalus is linked to the main grooved facet but is not visible in the nilgai.

The metatarsals of *M. acrae* are more like the metatarsals of tragelaphines than those of alcelaphines. The anterior longitudinal grooves are pronounced and, although their distal termini are medially situated, they are arched along

Fig. 22. Proximal articular surfaces. From above: L 13071 right metacarpal. L 7625 right metatarsal. L 20508 left metatarsal. Anterior edges lie towards the top of the page.
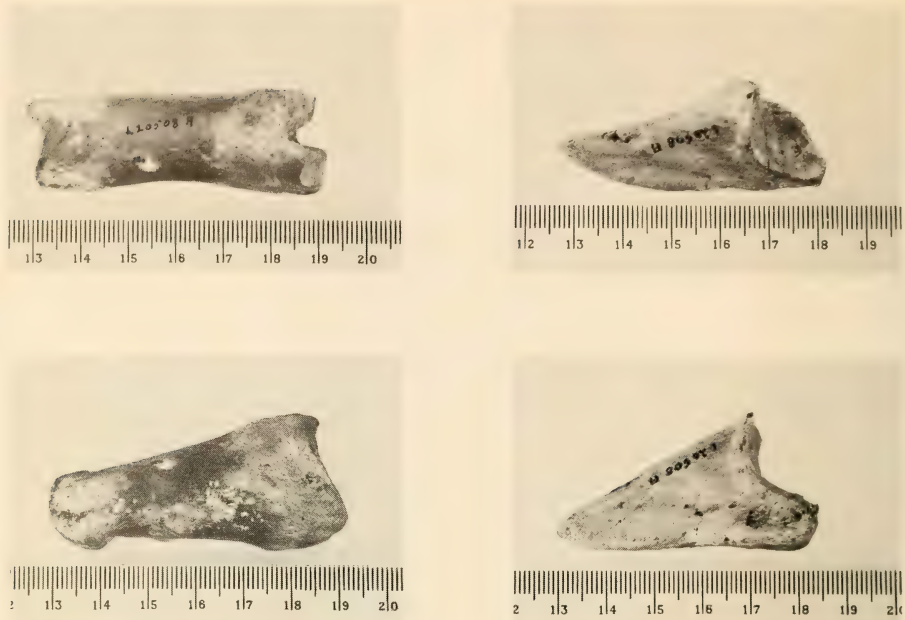
Fig. 23. L 20508. 1st phalanx in dorsal view (above) and outer view (below). 3rd phalanx in dorsal view (above) and outer view (below).

their length towards the lateral edge of the shaft (a, Fig. 21), and their proximal termini are a little off-centre. The metatarsal III elements are thus a more prominent part of the anterior surfaces than the metatarsal IV elements. Tragelaphines, but not the nilgai, also exhibit these characteristics and, although they might be quite pronounced in the eland, the asymmetry is apparently never as extreme as in the *M. acrae* specimens. The secondary (posterior) naviculocuboid facets of the proximal surface are transversely elongated (b, Fig. 22) as in the tragelaphines and nilgai, and the posterior part of the articular surface is consequently broader than in alcelaphines and other cursorial bovids (see Gentry 1970: 280). The posteriorly situated facet for articulation with the vestigial metatarsal is more prominent than usual in tragelaphines but less so than in alcelaphines, and thus resembles the nilgai. As in the metacarpal, the posterior hollows above the distal condyles are deep.

The first and third phalanges of *M. acrae* (L 20508, L 14081) are more stoutly proportioned than those of the greater kudu but are not as heavily built as in the eland.

Measurements of the Langebaanweg limb bones are given in Table 2.

Table 2

	Humerus L 13071	Radius L 13071	Metacarpal L 13071	Metacarpal L 12811	Metatarsal L 20508	Metatarsal L 20334	Metatarsal L 7625
Overall length	260,0	c.290,0	c.266,0	c.264,0	270,0	c.254,0	263,0
Maximum transverse diameter at proximal end . .	75,0	60,5	48,9	51,8	40,1	41,4	39,8
Maximum antero-posterior diameter at proximal end	77,5	33,5	32,2	34,2	38,2	42,0	42,9
Least transverse thickness of shaft	30,5	33,0	c.28,0	—	23,5	—	c.26,0
Maximum transverse diameter at distal end . . .	61,2	56,9	50,2	—	40,5	45,6	47,7
Maximum antero-posterior diameter at distal end . .	60,7	40,9	33,6	—	31,8	31,8	32,2

The relative lengths of the radius and metacarpal against the humerus, and the least transverse thickness across the shaft of the humerus, radius and metapodials are shown in Figures 24 and 25. In these figures the Langebaanweg bones are compared with the following similarly-sized antelopes:

Tragelaphus eurycerus	bongo	symbol	r
Tragelaphus strepsiceros	greater kudu	,,	u
Boselaphus tragocamelus	nilgai	,,	n
Connochaetes taurinus	blue wildebeest	,,	o
Alcelaphus buselaphus	hartebeest	,,	x

The bongo lives in forests, the greater kudu is most typically an inhabitant of hilly country with thickets preferably near rivers, the nilgai lives in areas with scrub or open woodland, and the wildebeest and hartebeest are cursorial antelopes of open plains. In the first three species the humerus is relatively thin and the radius relatively short, and the bongo has a noticeably short metacarpal and a thick radius and metapodials. The metapodials of the wildebeest are thicker than in the hartebeest, and the metacarpal of the hartebeest is notably long. The proportions of the limb bones thought to be of *M. acrae* follow fairly well those of the greater kudu and the nilgai. It is therefore unlikely from this evidence that the species was either a forest inhabitant or a cursorial plains-dweller. More probably it lived in an intermediate habitat of thicket, scrub or open woodland.

COMPARISONS

The tribe Boselaphini belongs to the subfamily Bovinae, which also contains the larger and more specialized Bovini and the African tribe Tragelaphini. Both the latter probably have a boselaphine ancestry. It is clear that *Mesembriportax* is not a bovine or tragelaphine but a boselaphine which developed some specializations of its own and retained some different primitive characters from tragelaphines or bovines. It differs from Tragelaphini by its non-spiralled or scarcely-spiralled horn cores, their medio-lateral compression, the specialized distal part of the horn core, the strong temporal ridges, large preorbital fossa, basioccipital not long or transversely constricted in its centre, and small central incisors. It differs even from the early or primitive bovines *Parabos* Arambourg & Piveteau, 1929 of Europe, *Proamphibos* Pilgrim, 1939 of the Siwaliks, and *Ugandax* Cooke & Coryndon, 1970 of Africa by its smaller size, horn cores with medio-lateral compression and more upright insertions, distal part of the horn core with a sharply reduced cross-section, back of the skull less widened, flatter lateral walls of upper molars and medial walls of lowers, and central cavities of upper molars somewhat simpler.

It differs from the living nilgai, *Boselaphus tragocamelus*, by a wealth of characters, among which it is sufficient to mention the longer horn cores with
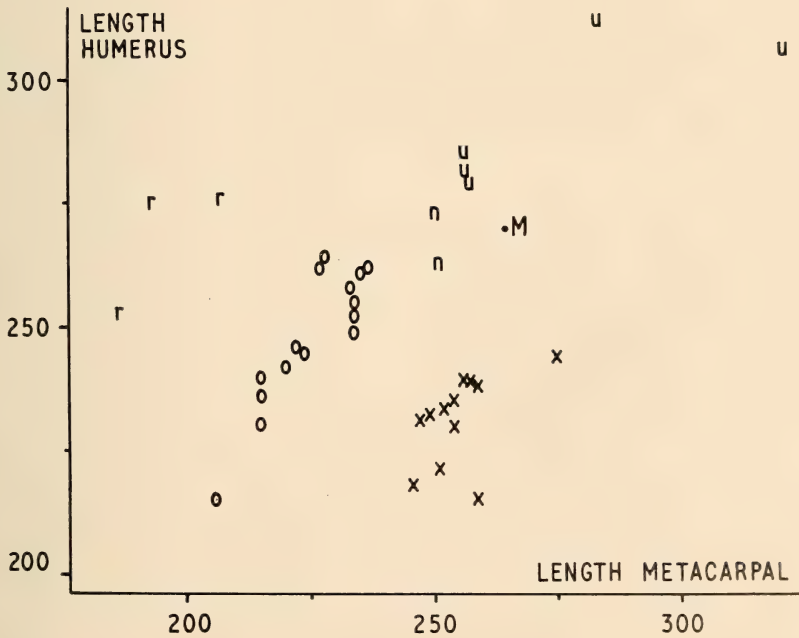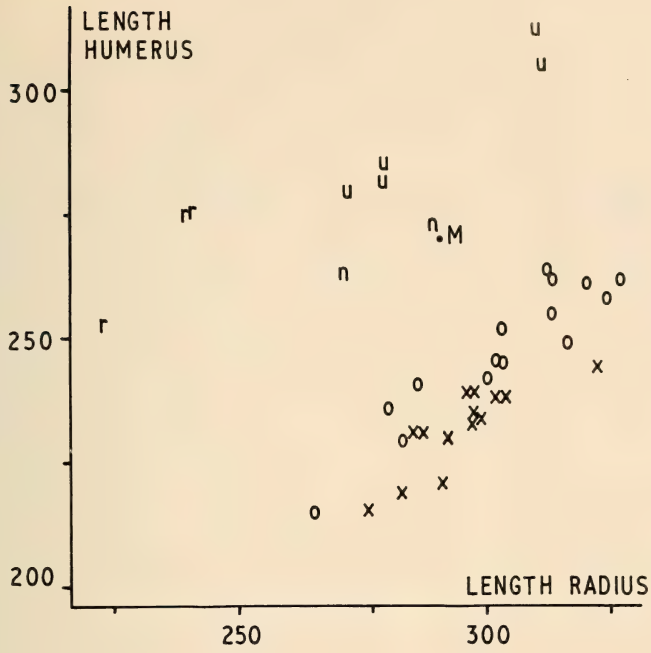
Fig. 24. Graph of humerus length plotted against radius length and metacarpal length. Scales are in millimetres. 'M' marks *Mesembriportax acrae*, and other symbols are explained in the text.

METATARSAL
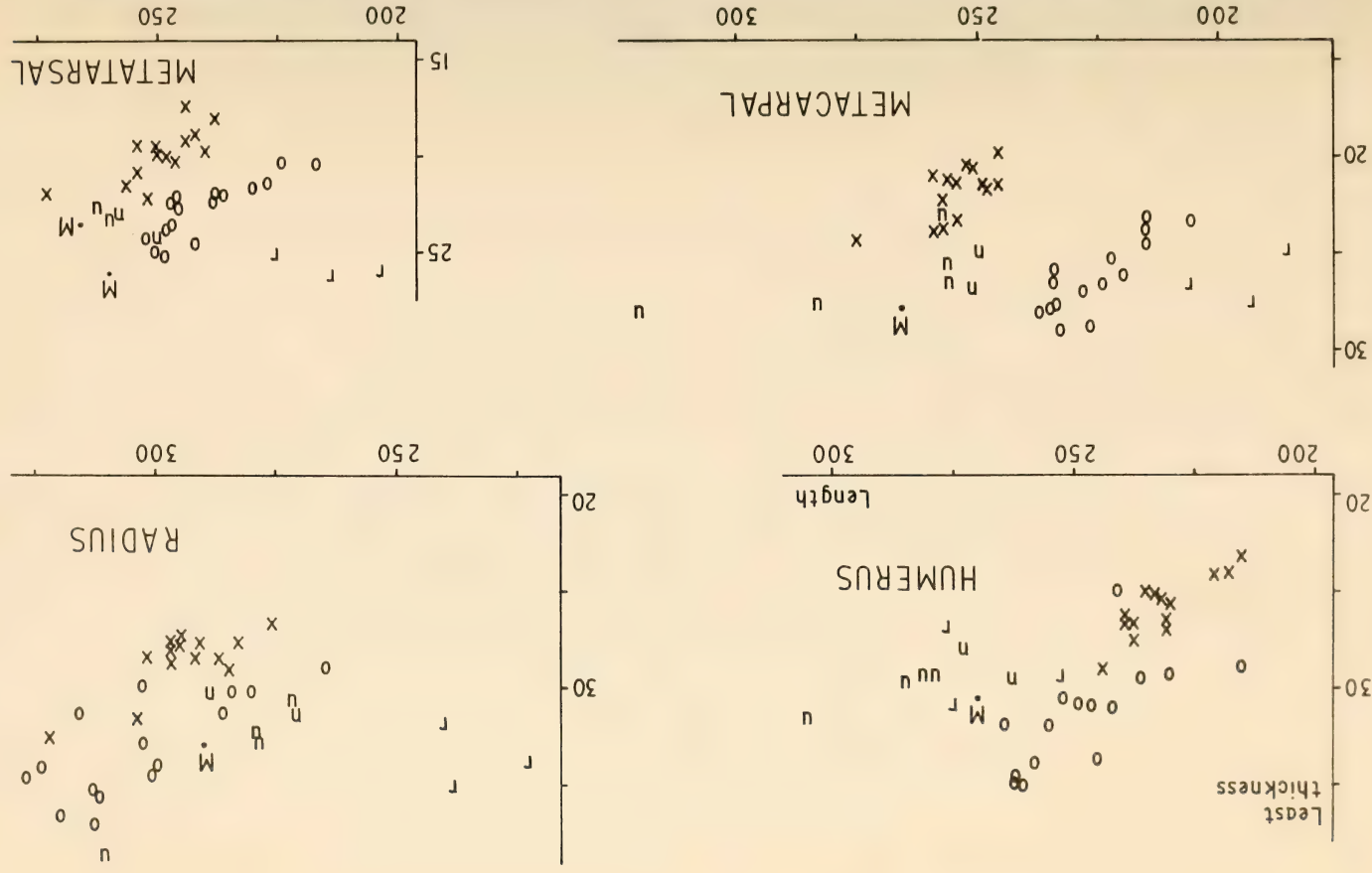
METACARPAL

RADIUS

HUMERUS

Length

Least thickness

Fig. 25. Graphs of length (horizontal axes) against least transverse thicknesses of the shafts (vertical axes) for four limb bones.
Scales are in millimetres, and symbols as in Fig. 24.

an anterior keel ending well below the tip, the horn cores inserted above and not behind the orbits, the extensive sinuses within the frontals, central cavities of molars V-shaped rather than curved, flatter lateral walls of upper molars and medial walls of lowers, longer premolar row and wider premolars, shorter diastema, deeper horizontal ramus of mandible, and fewer cursorial characters in the limb bones. Its much larger size and the possession of only two horns rule out any close relationship to *Tetracerus quadricornis*. Allometry would hinder further comparison between these two forms.

Gentry (*in* Hendey 1970*a*: 114) had suggested that the first discovered horn core pieces of *Mesembriportax acrae* might belong to *Miotragocerus* or *Protragocerus*, both of them Upper Miocene boselaphines. The fuller material now available suggests that comparison of *M. acrae* should be made with the following extinct boselaphines:

Pachyportax Pilgrim, 1937

> *P. latidens* (Lydekker, 1876) of the Dhok Pathan and possibly the Tatrot Formations, Siwaliks Hills
>
> *P. nagrii* Pilgrim, 1939 of the Nagri Formation. Siwaliks Hills

Selenoportax Pilgrim, 1937

> *S. vexillarius* Pilgrim, 1937 of the Nagri Formation

Protragocerus Depéret, 1887

> *P. chantrei* Depéret, 1887 from the European Upper Miocene
>
> *P. gluten* (Pilgrim, 1937) from the Chinji and lowest Nagri Formations
>
> *P. labidotus* Gentry, 1970 from Fort Ternan, Kenya and dated to 14 million years (Bishop, Miller & Fitch 1969: 685)

Miotragocerus Stromer, 1928

> The more familiar name *Tragocerus*, used until recently for this genus, was discovered by Kretzoi (1968) to be preoccupied by a beetle, and Gentry (1971: 284 footnote) suggested *Miotragocerus* in its place. It contains the following species and perhaps others:
>
> *M. gradiens* (Pilgrim, 1937) of the Chinji Formation
>
> *M. leskewitschi* (Borisiak, 1914) of Sebastopol, Russia
>
> *M. amalthea* (Roth & Wagner, 1854) from Pikermi, Greece, and elsewhere
>
> *M. valenciennesi* (Gaudry, 1865) a smaller Pikermi and Samos species
>
> *M. browni* (Pilgrim, 1937) of the Dhok Pathan Formation
>
> *M. spectabilis* (Schlosser, 1903) of the Chinese mid-Tertiary

Tragoportax Pilgrim, 1937

> *T. salmontanus* Pilgrim, 1937 of the Dhok Pathan Formation

The comparison of *Mesembriportax acrae* with the first two genera of this list is not a matter of difficulty. *Pachyportax nagrii* is a species of only doubtful

validity, having as holotype a hornless female cranium. *P. latidens* is best represented by a cranium, *P.l. dhokpathanensis* Pilgrim, 1939, in Calcutta, of which there is a cast in London. From this it can be seen that *M. acrae* is about the same size as *P. latidens* but has horn cores more strongly compressed medio-laterally, with a stronger anterior keel, inserted more uprightly and having greater divergence. The frontals are raised and have more extensive internal hollowing, the bone surface between the temporal ridges is more rugose, the orbits are without a dorsal rim, the braincase is more angled on the face axis and widens posteriorly, and the nuchal crests are weaker.

Selenoportax vexillarius is a large boselaphine among its contemporaries. The holotype is a cranial roof with horn cores from the Nagri Formation, and only referred teeth are known from the Dhok Pathan Formation. These teeth, along with the holotype juvenile maxilla and referred teeth of a supposed second species *S. lydekkeri* (Pilgrim, 1910), must be regarded as of uncertain identity. *M. acrae* differs from the *S. vexillarius* holotype by its horn cores being shorter, more compressed medio-laterally, with the insertion of the anterior keel not rotated to a medial position, no postero-medial keel, with a reduced circular cross-section in their distal part, the frontals between the horn cores higher than the orbits' dorsal edges, a rugose surface between the temporal ridges, the orbits without projecting dorsal rims, smaller supraorbital pits, the braincase more angled on the face axis, and weaker nuchal crests. The state of internal hollowing in the frontals of *S. vexillarius* is not known, but the available space must have allowed much less than in *M. acrae*. Like *Pachyportax*, *Selenoportax* appears to be an independent boselaphine lineage with no particular relationship to *M. acrae*.

The question of the relationship of *M. acrae* to the last three genera can only be answered within the context of an assessment of how they are related among themselves. *Protragocerus* has been diagnosed by Gentry (1970: 246). It is an early form with such primitive characters as small size, no internal sinuses in the frontals, as much as half of the braincase roof curving downwards posteriorly, no rugosity of the bone surface between the temporal ridges, prominent nuchal crests, and a small basioccipital with but poor development of the anterior tuberosities.

P. labidotus is the most completely known species; it has horn cores with a marked accentuation of their antero-posterior diameter in their lower parts and hence a strong degree of medio-lateral compression, a clearly demarcated terminal portion of the horn core above the top of the anterior keel with a much smaller cross-sectional area, and the horn pedicels becoming extended antero-medially by the development of ridges. *P. labidotus* also shows persisting canine alveoli between the maxillae and premaxillae, and this would probably be seen also in other species were that part of their skulls known. *P. chantrei*, the type species, is very poorly known; it has horn cores with less antero-posterior elongation and hence less medio-lateral compression and less differentiation of a terminal portion, and no ridges on the horn pedicels.

P. gluten, in which Gentry (1970) sank a number of other Siwaliks named forms, needs further interpretation. The holotype and the conspecific cranium of *Strepsiportax chinjiensis* Pilgrim both have horn cores with a less exaggerated antero-posterior diameter than *P. labidotus*, and are thus less medio-laterally compressed. The main keel at the back is situated postero-laterally. Gentry (1970: 257) synonymized *Helicoportax praecox* and *H. tragelaphoides* with *P. gluten*, but perhaps minimized their differences from the latter. The holotype partial skull of *H. praecox* Pilgrim (1937, figs 6, 7, 62), the holotype horn core of *H. tragelaphoides* Pilgrim (1939, pl. 4 figs 3, 3a), and two other right horn core bases, British Museum (Natural History) M. 15469 and M. 15470, all have larger horn cores than the *P. gluten* holotype (Pilgrim 1937, figs 12–17). In their lower parts the strongest keel at the back is the postero-medial and not the postero-lateral one, and there is more of a transverse ridge across the frontals between the horn bases. Correlated with the strengths of the two posterior keels, the medial surfaces of the horn cores are more flattened than the lateral ones. More distally the postero-lateral keels retain their dominance, and the cross-sections are closer to that of the *P. gluten* holotype. The '*Helicoportax*' specimens may simply be ontogenetically older than *P. gluten*, or they may deserve sub-specific rank as *Protragocerus gluten praecox* (Pilgrim). Such a subspecies would not necessarily include the female cranium figured as *H. praecox* by Pilgrim (1937, figs 8–11). If the subspecies is valid, it may be a temporal transition from *P. gluten* to the Nagri *Selenoportax vexillarius* as was thought by Pilgrim himself. It may yet be shown that *P. gluten gluten* survived to give rise to some other boselaphine, such as *Pachyportax latidens*. *Sivoreas eremita* Pilgrim (1939: 131, pl. 4 figs 1, 1a) may belong to *P. gluten*. Gentry (1970: 259) supposed it was antilopine, but was later more doubtful (Gentry 1971: 289). This doubt remains, but while the holotype frontlet and an assigned horn core piece, British Museum (Natural History) M. 15495, show a high degree of spiralling, two other horn core bases, also numbered M. 15495, are rather difficult to distinguish from *Protragocerus*. Certainly there is no case for regarding *S. eremita* as tragelaphine, which was Pilgrim's view.

P. gluten differs from *P. labidotus* by a slightly lower and wider skull, longer horn cores with no basal enlargement of the antero-posterior axis and scarcely any differentiation of the distal portion, and no ridges on the pedicels.

Miotragocerus can be told from *Protragocerus* by its horn cores having less torsion, being inserted less widely apart, sometimes by its higher and narrower skulls, and probably (see Thenius 1951: 278) by having hollowed horn core pedicels. *Miotragocerus leskewitschi* is a species with a number of primitive characters. The downwards curvature of the back of the braincase roof (less pronounced than in *Protragocerus*), the smallness of the basioccipital and its poorly developed anterior tuberosities may be mentioned in particular, and the rather small overall size, short horn cores, and lack of much surface rugosity between the temporal ridges, may also be primitive. Its nuchal crests are not strong, and the tip of the horn core has smaller cross-sectional areas than the

more proximal part. Whether it is actually early for a *Miotragocerus* depends on the dating of Sebastopol, which is discussed in Van Couvering & Miller 1971 and Van Couvering 1972. *M. amalthea* is a larger species with somewhat longer horn cores in which the distal portion has a small cross-sectional area, the frontals have some internal sinuses, and there is an upstanding transverse ridge between the horn pedicel bases. There is still not a great development of surface rugosity between the temporal ridges. The basioccipital is larger than in *M. leskewitschi* and has scarcely any development of a central longitudinal groove. The skull is more definitely low and wide than in *M. leskewitschi* and the horn cores show some degree of torsion, both of which are approaches to *Protragocerus*. *M. monacensis* Stromer and *M. pannoniae* (Kretzoi) are names which have been applied to more north-westerly occurring examples of the genus. Illustrations of them (Stromer 1928, fig. 1; Thenius 1948, figs 1, 2; Tobien & Jörg 1959, pl. 11) show short straight horn cores without much torsion but with terminal portions of abruptly smaller cross-sectional area, stronger rugosity of the bone surface between the temporal ridges than in *M. amalthea*, a little downwards curvatures at the back of the braincase roof, and the premaxilla rising with even width to make contact with the nasals. *M. valenciennesi* is a scarcely known smaller species than *M. amalthea*, found at Pikermi and Samos, and there is also perhaps a larger species at these sites (Gentry 1971: 243). Some *Miotragocerus* at Samos differ from *M. amalthea* in having longer horn cores, with less torsion and most probably with no demarcation of their distal part; they may also have the braincase more angled on the face axis. They have received the names *M. curvicornis* (Andree 1926) and *M. recticornis* (Andree 1926). A similar skull in the American Museum of Natural History, 20566, comes from quarry 5 at Samos, which may be later than other sites on that island (Gentry 1971: 280). *M. gradiens* is a small, primitive-looking species with some similarity to *M. leskewitschi*, but it has a narrower skull and slightly more upright horn cores, both of which must have helped to distinguish it from the contemporaneous *Protragocerus*. *M. vedicus* (Pilgrim 1939: 244) appears very similar to *M. gradiens* but comes from the later Dhok Pathan Formation; possibly it is an ontogenetically young specimen of a later species. *M. browni* (Pilgrim 1937: 781) is a later Siwaliks species apparently smaller than *M. amalthea*, although Pilgrim (1939: 217) was inclined not to stress this. It may or may not be conspecific with *M. punjabicus* Pilgrim, 1910. It has a higher and narrower skull than the European forms, and the holotype shows long horn cores curving backwards and without a terminal portion of small diameter. The rugosity of the frontals is not well marked. *M. spectabilis* of China is not well differentiated from *M. amalthea*.

Tragoportax salmontanus in the opinion of Gentry (1970: 259) includes material of two other supposed species from the Siwaliks. *Tragoportax aiyengari* Pilgrim (1939: 228, fig. 24) was founded on a cranium with horn core bases said to be from the Dhok Pathan Formation. A plaster cast of this cranium is available in London, and it differs from *T. salmontanus* by being larger, having

more upright horn core insertions in side view and a less pronounced transverse raising of the frontals between the horn bases. It does not seem sufficiently different from *T. salmontanus* to justify specific rank. Other Dhok Pathan remains have been referred to *T. islami* Pilgrim (1939: 230, figs 25d–f, 26). The holotype is a partial cranium, of which a plaster cast is available in London. The transverse narrowness of the cranium makes it doubtful that it comes from a *Tragoportax* rather than a *Miotragocerus*, and the remaining horn cores cannot be separated convincingly from *T. salmontanus*. *T. salmontanus* is smaller than *M. amalthea* and has fairly short horn cores probably without a distinct terminal portion, horn cores inserted close together and with an upstanding transverse ridge of the frontals between the bases, internal sinuses of the frontals, a strongly rugose surface between the temporal ridges, the back of the braincase a little down-curved posteriorly, and a basioccipital with a longitudinal groove extending forwards to pass between the anterior tuberosities. *T. salmontanus* is obviously a member of the *Protragocerus-Miotragocerus* group, but it is questionable whether it deserves separate generic rank. It is different from *Protragocerus* in the closeness of the horn core insertions, the raised ridge between the pedicels, the lack of a distinct terminal portion of the horn core, the braincase widening posteriorly, the rugosity of the bone surface between the temporal ridges, and the larger basioccipital with its more pronounced central groove. There are fewer differences from *Miotragocerus* which is a more diverse genus.

Mesembriportax acrae differs from *Protragocerus* by its greater size, horn core insertions less inclined backwards, the greater divergence of the horn cores, the internal sinuses of the frontals raising them well above the level of the top of the orbits, no dorsal rim to the orbits, the braincase roof angled and not curving downwards posteriorly, braincase widening posteriorly, a rugose surface between the temporal ridges, and a relatively larger basioccipital with stronger anterior tuberosities. It differs from *P. labidotus* by less extreme compression of the horn cores, the absence of a projecting anterior ridge on the horn pedicels, temporal ridges wide apart posteriorly, weaker nuchal crests, nasals without lateral flanges anteriorly, lower molars with straighter medial walls and occasional incipient goat folds, a longer premolar row (Fig. 26), a more massive metaconid on P_4, a closer approach of metaconid and paraconid on P_4, and more reduced canine alveoli at the maxilla/premaxilla junction. Many of these differences can be seen as evolutionary advances: greater size, frontals' sinuses, profile and rugosity of braincase roof, less marked nuchal crests, the basioccipital characters and the disappearance of the canine alveoli. The tooth characters, particularly the relative lengthening of the premolar row, cannot be so easily seen as advances.

Mesembriportax acrae differs from all *Miotragocerus* by having horn cores inserted more widely apart and with greater divergence, more extensive frontals' sinuses, orbits without dorsal rims, and the braincase more angled on the facial axis. It differs from all except *M. amalthea* by its greater size, horn cores with more torsion, and braincase widening posteriorly. It differs from *M. amalthea*
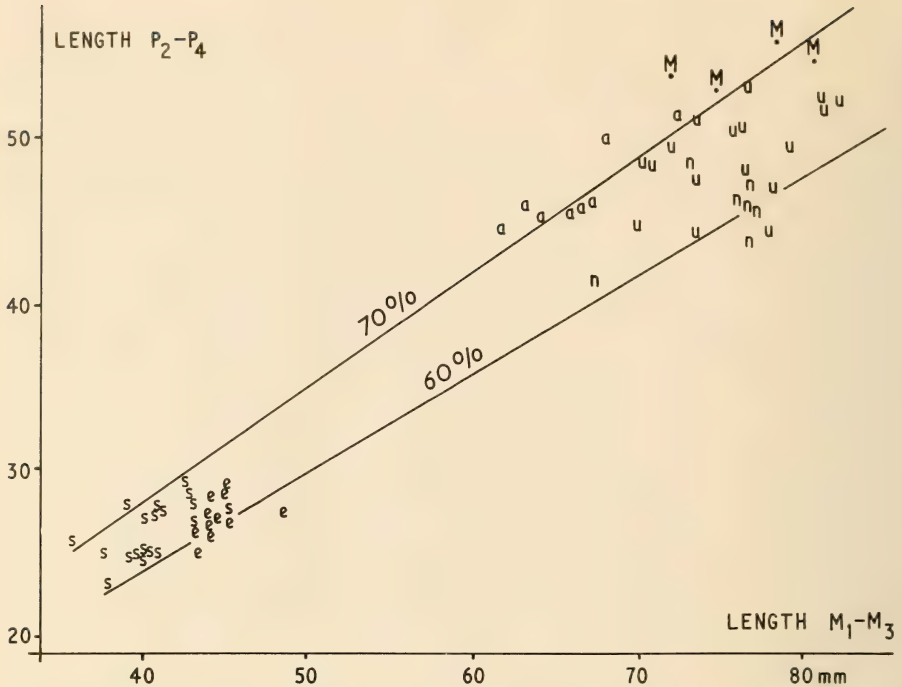
Fig. 26. Graph of length of lower premolar row against lower molar row. a = *Miotragocerus amalthea* from Pikermi, e = *Protragocerus labidotus*, n = *Boselaphus tragocamelus*, s = *Tragelaphus scriptus*, u = *Tragelaphus strepsiceros*, M = *Mesembriportax acrae*. The upper diagonal line passes through points along which the length of the premolar row is 70% of that of the molar row, and the lower one is the corresponding line for 60%.

by having less tendency to a postero-medial keel on its horn cores, and perhaps more of a rugose surface between its temporal ridges. It differs from *M. browni* by the wider skull, shorter horn cores which are less curved backwards, with less of a tendency to a postero-medial keel, and with the anterior keel terminating well below the horn core tip. There are other differences of *Mesembriportax acrae* from the more primitive-seeming *Miotragocerus gradiens* and *M. leskewitschi*. It is interesting that the plate of a *Miotragocerus* skull in Tobien & Jörg (1959, pl. 11) shows a premaxilla rising with even width to make a contact on the nasals, as in *Mesembriportax acrae* and *Protragocerus labidotus*. This bone conformation may be primitive in Boselaphini.

Definitely identified upper and lower dentitions of *Miotragocerus* are known, from which *Mesembriportax acrae* differs by the straighter medial walls of its lower molars. The P_4 of the *M. acrae* holotype differs in its more massive metaconid with less differentiation into a neck and strong anterior and posterior flanges, the paraconid assuming the shape of a low protuberance from the parastylid rather than a flange, and the hypoconid projecting more strongly than in many *Miotragocerus*. However, in L 20508 (Fig. 10) only the

last difference appears valid. The premolar row is about as long as in *M. amalthea* from Pikermi (Fig. 26).

Mesembriportax acrae differs from *Tragoportax salmontanus* by being larger, the top of the anterior keel terminating well below the tip on the horn core, the horn cores inserted more uprightly and further apart, the greater divergence of the horn cores, the expanded internal sinuses of the frontals and the orbits without a projecting dorsal rim, the braincase more angled on the face axis, the braincase roof not curved downwards posteriorly, temporal ridges not approaching so closely posteriorly, and the central longitudinal groove on the basioccipital not extending forwards between the anterior tuberosities.

Mesembriportax acrae seems to be a fairly isolated form by the huge extent of its frontals' sinuses and by other characters of the skull top and horn cores. The wide palate may also be notable. It could perhaps have descended from the Fort Ternan *Protragocerus labidotus*, which has horn cores with quite strong torsion, wide insertions, medio-lateral compression, and a long terminal part of small cross-section. The development of such distinctive horn core tips would be unique outside *Miotragocerus*, and only occurred in an area south of the known range of *Miotragocerus*. The main problems with such a hypothesis of descent are what could have happened to the anterior ridges of the horn pedicels and whether the premolar row could have lengthened. *Mesembriportax acrae* seems rather further from *Miotragocerus*, which has narrower skulls (with the possible exception of *M. amalthea*) and more closely inserted horn cores with generally less torsion. Its wide horn core insertions and the basioccipital morphology suggest that it is not close to *Tragoportax salmontanus*. A tentative phylogeny is shown in Figure 27.
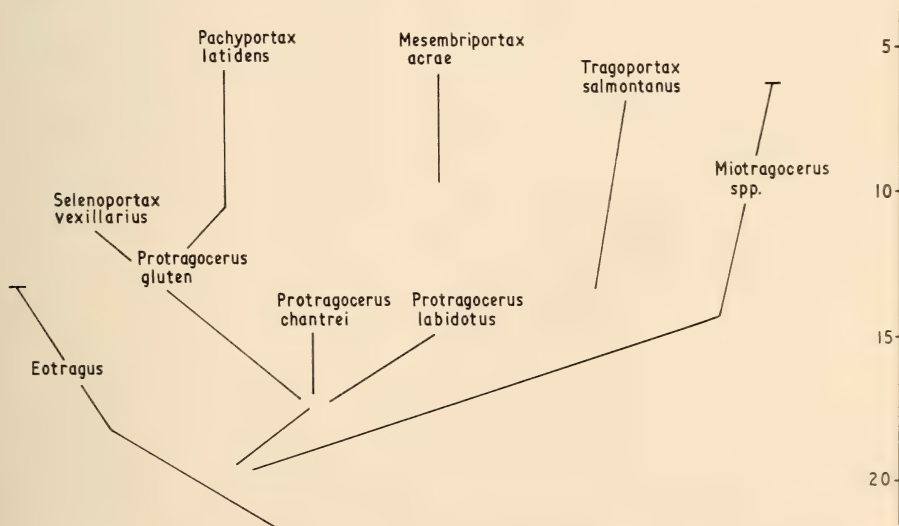

Fig. 27. Phylogeny for some Boselaphini. The time scale is in millions of years. The origins of Bovini, Tragelaphini and the two living boselaphines are too questionable to be shown here.

Character	State	1	2	3	4	5	6	7	8	9	10
Hc. torsion	present/little or absent	−		+	+	+	−		−	+	+
Hc. pedicels	no anterior ridge/with one	+	+	+	+	−		+	+	+	+
Frontals raised between hc. bases	raised/not raised	−	−	−	−	−		+	+	+	+
Frontals with internal sinuses	extensive/poorer	−	−	−	−	−		+	+	+	+
Bone surface between temporal ridges	rugose/smoother	+	−	−	−	−	+	−	−	−	+
Distance apart of temporal ridges	wide/close	+	+	+	+	−		−	+	+	+
Size of supraorbital pits	small/larger	+		−	+	+		+	+	+	+
Braincase angled on face axis	more/less	−	−	−	−	−	−	−	−	−	+
Braincase widens posteriorly	yes/no	−	−		−	−		−	−	−	+
Posterior cranial roof	nearly straight/curved down	+	+	+	−	−	−	−	+	−	+
Nuchal crests	not strong/strong	−	−	−	+	−	+	−	+	+	+
Size of basioccipital	large/smaller	+	+		−	−	−	−	+	+	+
Central longitudinal groove on basioccipital	absent/present	−	+		+	+	+	+	+	+	+
	No. of differences (−) from *M. acrae* (+)	12	8	11	12	13	12	12	7	12	10
	No. of characters compared	25	20	22	25	25	22	25	25	25	25
	Preceding fractions converted to percentages	48	40	50	48	52	55	48	28	48	40

Hc. = horn core.

PHENETIC COMPARISONS

A simple quantitative assessment of the phenetic differences of *Mesembriportax acrae* from other boselaphines was undertaken, slightly modified from the method of Corbet & Hanks (1967: 50). The results of such a straightforward, unweighted morphological comparison, taking no account of time, phylogeny or allometry, are interesting in comparison with the findings just stated above.

Table 3 is a list of non-metrical characters in which the species differ. The data is taken from material and casts in the British Museum (Natural History) and from published illustrations. Tooth characters are omitted since they are available only for *Mesembriportax acrae*, *Protragocerus labidotus*, *Miotragocerus amalthea*, *M. leskewitschi* and the nilgai. The state of the characters in *Mesembriportax acrae* has been designated by a + sign, and the opposite state for each character by a − sign. In the column headed 'state', the first alternative describes the character in *M. acrae*. No allowance has been made for intermediate states, and blank spaces are left where characters cannot be determined on available material. Numerical values can then be given to the character states: $+ = 1$, $- = 0$, and the sum of differences of *M. acrae* from each of the comparative species is shown at the foot of the columns of Table 3, expressed as a fraction of what the total score would have been if the two species had differed in every character. Normally this total is 25, but the incompleteness of some fossils reduces it to 20 or 22. The fractions are standardized as percentages in the lowest line of the table.

TABLE 4

Percentage differences between pairs of boselaphine species.

		1	2	3	4	5	6	7	8	9	10
1	*Boselaphus tragocamelus*										
2	*Pachyportax latidens*	30									
3	*Selenoportax vexillarius*	32	18								
4	*Protragocerus gluten*	40	35	41							
5	*Protragocerus labidotus*	52	35	55	20						
6	*Miotragocerus gradiens*	59	56	79	32	23					
7	*Miotragocerus leskewitschi*	56	45	68	24	20	9				
8	*Miotragocerus amalthea*	44	35	45	28	40	41	28			
9	*Miotragocerus browni*	40	40	55	40	60	36	40	28		
10	*Tragoportax salmontanus*	48	55	64	32	36	27	24	28	40	
11	*Mesembriportax acrae*	48	40	50	48	52	55	48	28	48	40

The top row of numbers indicates the same species as are listed on the left.

The percentage differences were then found between every pair of species in Table 3, and the resulting figures are given in Table 4. Figure 28 shows a dendrogram of phenetic differences based on the percentages in Table 4; in this dendrogram the positions of the linking lines between any two clusters represent the mean difference between all members of one cluster and all members of the other cluster.

Several interesting observations arise from these exercises.

1. According to Table 3, *M. acrae* is phenetically remote from the early genus *Protragocerus*, from three of the four *Miotragocerus* species, from *Selenoportax vexillarius*, and from the nilgai. Percentage differences from all these forms are 48 or above.

2. It is least different from *Miotragocerus amalthea*, being quite pronouncedly closer to it than to any other species. This is a surprising contrast to the hypothesis of descent from a *Protragocerus* species. Even if tooth characters were taken into account, as is possible for these three species, the percentage differences from *M. amalthea* and *P. labidotus* would only change to 31 and 57 respectively. However, Table 4 shows that *M. amalthea* has no large and no small percentage differences from any other species. Its total range of readings extends only from 28 to 45, compared with 9 to 68 for *M. leskewitschi* or 18 to 79 for *Selenoportax vexillarius*. It seems to be very much an 'average' boselaphine. Not only does it have no linkage lower than 28 to any other species, but it links simultaneously with four species at that level. Its closeness to *Mesembriportax acrae* should be judged only in conjunction with these reservations.

3. Tables 3 and 4 confirm that *Mesembriportax acrae* is a well-marked form, and support its attribution to a new genus.

4. Concerning the other species used in the phenetic comparisons and shown in Figure 28, it may be noted that the species pairs *Pachyportax latidens*
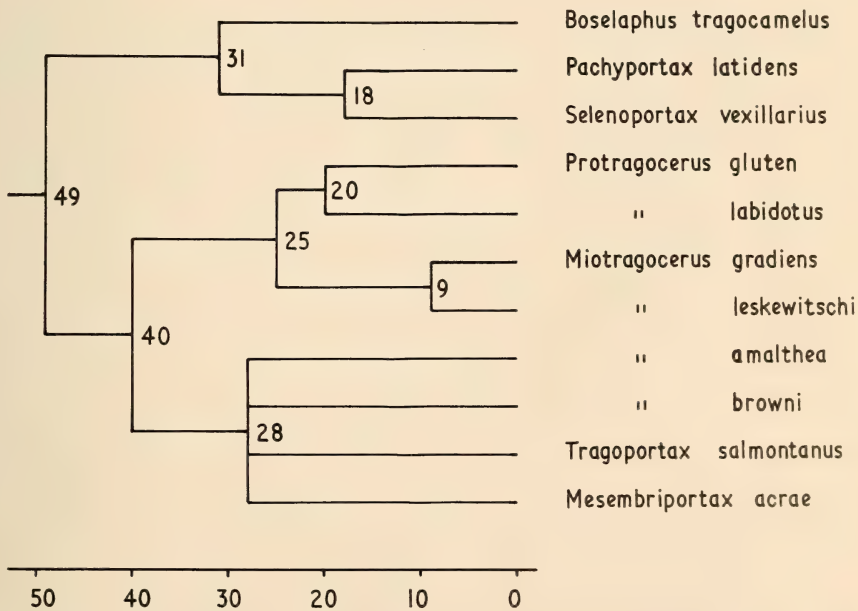

Fig. 28. Dendrogram of phenetic differences between some Boselaphini.

with *Selenoportax vexillarius*, the two *Protragocerus* species, and *Miotragocerus gradiens* with *M. leskewitschi* are convincing or plausible phyletic groupings. The same may also apply to the further link of the nilgai with *Pachyportax* and *Selenoportax*. This takes place at the 31 level, which is quite a lot lower than the nilgai's link with any other species. The complete central cluster joined at 25 is a union of early, primitive or small boselaphines, and this imposes a 'horizontal' rather than a 'vertical' arrangement of species in the rest of the dendrogram. It leaves the bottom four species as a cluster of larger and later or more advanced boselaphines. It is doubtful whether even the two *Miotragocerus* species and *Tragoportax salmontanus* in this later group are phyletically closer to each other than to *M. gradiens* or *M. leskewitschi* in the preceding cluster. Indeed, *T. salmontanus* would have had closer links with *M. leskewitschi* and *M. gradiens* at 24 and 27 respectively had they not already joined *Protragocerus*. The inclusion of *Mesembriportax acrae* in this phenetic group is a clear clash with the phyletic interpretation presented in this paper, and may be attributed to parallel evolution and to the fact that *Miotragocerus amalthea* happens to link with several species at the 28 level.

The numerical phenetic comparison has been useful in emphasizing the close morphological resemblance of *Mesembriportax acrae* to *Miotragocerus amalthea*, but the results of such a comparison must evidently be interpreted very carefully when applied to taxa of different overall body size and different time levels.

CONCLUSION

Mesembriportax acrae has been seen to have several interesting specializations, most notably those associated with the frontals and horn cores. It has very divergent horn cores, possibly with bifurcated sheaths, inserted widely apart on frontals which possess an extensive system of internal sinuses.

It may have descended from a boselaphine like *Protragocerus labidotus*, but in doing so it evolved some cranial characters in parallel with *Miotragocerus amalthea*, well known from the Upper Miocene of Europe.

It has been shown that the morphology of the teeth of *Mesembriportax acrae* agrees broadly with the boselaphines and tragelaphines, but that the premolar row is rather long, particularly in comparison with the nilgai. This might indicate a wholly rather than a partly browsing diet. The limb bone proportions are nearer to both nilgai and greater kudu than to antelopes of open plains or thick forests, and the morphology of the limb bones is more like the greater kudu than the nilgai. So far as can be judged from written comments, the nilgai may differ ecologically and behaviourally from the greater kudu by living in terrain which is less hilly and more open, and by being partially a grazer instead of predominantly a browser (Prater 1965: 273; Schaller 1967: 171; Dorst & Dandelot 1970: 194; Wilson 1965). It is possible that *M. acrae* was nearer to the greater kudu pattern of life. However, as a Pliocene antelope it could have had less highly evolved adaptations for a nilgai-like ecology.

SUMMARY

Some well-preserved fossils of a new genus and species of a boselaphine antelope, *Mesembriportax acrae*, are described from the Pliocene of Langebaanweg, Cape Province, South Africa.

ACKNOWLEDGEMENTS

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